

BOOKS, PERIODICALS & PAMPHLETS

The Cowry n.s.

JIRI ZIDEK, editor. Volume 1, number 1, 24 pp., quarto, May 1994. ISSN 0574-3737.

From the front cover: "*The Cowry* of Lt.-Col. R. J. Griffiths commenced in 1960 and ceased publication in 1968. It was devoted solely to the living Cypraeidae. The current journal honors Lt.-Col. Griffiths' effort by retaining the name and broadens his aim by encompassing the entire superfamily Cypraeacea and the related Velutinae. It is an international refereed journal that publishes both neontological and paleontological contributions on all aspects of the taxonomy, biology and phylogeny of these groups and accepts color illustrations. Contributions include, but are not limited to, original-research and review-type articles, short notes, pictorial accounts (variability, habitats, etc.), book reviews and literature notices." The editorial board includes members in the United States, New Zealand, Germany, and Holland.

Articles in the first issue include "Lt.-Col. R. J. Griffiths and his cowry journal" by J. Zidek and J. H. Black; "Catalog of fossil and Recent Cypraeidae and Eocypraeinae (Ovulidae) described since 1971" by L. T. Groves; "Beach-collecting cowries: possibilities and limitations" by W. Krommenhoek; and a section of editor's comments, including some words of gentle encouragement to potential contributors who may be uneasy about having their contributions reviewed by referees.

The journal evidently contemplates publishing descriptions of new taxa and requires that holotypes be deposited in public institutions and provided with catalogue numbers.

Frequency is semi-annual (May and November). An annual subscription is \$20 in the United States (\$25 elsewhere) for individuals and \$40 in the U.S. (\$45 elsewhere) for institutions. The journal is available from Dr. Zidek at P.O. Box 95, Socorro, NM 87801 USA (for subscriptions and correspondence), or at New Mexico Bureau of Mines & Mineral Resources, NM Tech C/S, Socorro, NM 87801 USA (for manuscripts).

B. Roth

Foregut Anatomy, Feeding Mechanisms, Relationships and Classification of the Conoidea (=Toxoglossa) (Gastropoda)

by JOHN D. TAYLOR, YURI I. KANTOR & ALEXANDER V. SYSOEV. 1993. *Bulletin of the Natural History Museum, London (Zoology)* 59(2):125-170.

The traditional family Turridae presents one of the most vexing problems in gastropod classification. It is enormously diverse, with more than 600 genera and some 10,000 Recent and fossil species described. This attribute and the prior reliance of taxonomists on few taxonomic characters have combined to inhibit the derivation of hypotheses of phylogeny by modern objective methodologies. It has long been recognized that this taxon needed to be subjected to a modern phylogenetic analysis based at least in part on anatomical characters, in addition to the shell and radular characters used in previous classifications. Not until completion of a broad survey of anatomy could there be sufficient evidence for changing the status of the numerous (11-17) subfamilies currently in use, although Morrison (1966) and McLean (1971) anticipated that changes in family-level classification would be the result.

Using information largely from their new comparative anatomical study of the foregut, Taylor, Kantor, and Sysoev have now presented the first phylogenetic hypothesis for the Superfamily Conoidea based on cladistic methodology. They also provide a detailed and well-documented basis for a revised classification of the family-group taxa previously assigned to the Turridae and to the other traditional families of Conoidea, the Terebridae, and Conidae. The rhynchodeum, proboscis, buccal mass, radular apparatus, and foregut glands provide 33 new anatomical characters, coded in 73 states. The authors present a cladistic analysis based on these and on 10 shell and operculum characters, the latter coded in 27 states.

Taylor, Kantor, and Sysoev diagnose the Superfamily Conoidea as having a venom gland and permanent rhynchodeum, the proboscis formed by elongation of the buccal tube, with the buccal mass located at its base, and a radular row primarily of five teeth but with the tendency to loss of the central and lateral teeth. They also provide a new classification of the superfamily, based in large part but not completely on their cladogram.

While a major accomplishment, the work under review is unfortunately difficult to use, partly because of its organization and partly because of the inherent complexity of the authors' task. To determine the characters that distinguish one family, subfamily or genus from another, the reader must work from the cladogram (with numbered nodes) and the new classification on p. 154, to the table of synapomorphies indicated by node number and character number (p. 153), to the tabular character analysis (p. 151), which decodes character and state numbers. A full character state matrix is given on p. 152. Taylor et al. illustrate 12 types of foregut morphology and then describe five types of feeding mechanism in Conoidea. The authors discuss representatives of each but the two sections are not well coordinated with each other, and they do not

explicitly indicate the distribution of these types among taxa. The new characters are generously illustrated, but the captions would have been more helpful had they indicated the family-group taxon of each genus illustrated.

Each family and subfamily in the authors' new classification is described in the section, "Diagnoses of Higher Taxa." These summarize shell, radula, and foregut characters but do not explicitly compare and contrast similar taxa in a way that would facilitate the challenging task of specimen identification. A table contrasts character states in the two subfamilies of Terebridae. Comparable tables for the reconstituted larger families Turridae and Conidae would have made the paper more user-friendly.

Because foregut anatomy constitutes their major contribution to the taxonomic database, Taylor et al. consider only the living Conoidea. In an appendix, they list all extant genus-group taxa and their new allocations. Type species and references for all Recent genera and subgenera described subsequent to Powell's (1966) monograph are given.

Although the Conoidea are well represented in Cretaceous and Tertiary strata, the work fails to mention the fossil record of any of the taxa. Of course such analysis would have to be restricted to the smaller set of shell characters, but it might have served to corroborate the phylogenetic analysis. Perhaps the authors intend to consider this at a later date. The omission of fossil genera in the appendix also impedes use of the new classification, because all available genera need to be taken into account when allocating taxa at the species level. An example is the omission of Olsson's (1964) Neogene genera from Ecuador, which Powell (1966) missed.

The phylogenetic tree of Taylor et al. incorporates vastly more information than the only prior cladistic analysis of the group, a primitive effort based solely on radular characters of turrid subfamilies and genera (Shimek & Kohn, 1981). In a particularly intriguing result, Taylor, Kantor, and Sysoev's phylogenetic analysis indicates that a widely considered characteristic feature of Conoidea, hollow marginal radular teeth that function as hypodermic needles to envenomate prey, originated independently at least five times in the evolution of this clade. We list these below, and we note their family-group status in the new Taylor et al. classification:

1. The large clade (indicated as Node 18 in Taylor et al.) including the subfamilies Coninae, Conorbinae, Clathurellinae, Oenopotinae, Mangeliinae, and Daphnellinae of the reconstituted family Conidae. (This clade also includes the subfamily Taraninae, interpreted as having lost the radula).
2. *Toxicionella* (Family Turridae, Subfamily Clavatulinae).
3. *Pilsbryspira* (Family Turridae, Subfamily Zonulispirinae).
4. Many members of the Family Terebridae.
5. *Imaclava* (Family Drilliidae). In cases 1–4 above, the

radula consists only of marginal teeth. In contrast, Drillidae retains the primitive radula character of five teeth per row fixed to a functional membrane. Hollow marginal teeth are an autapomorphy of the genus *Imaclava* and hence not shown in the Taylor et al. cladogram.

The new family-group classification of the Conoidea that Taylor et al. propose is quite unprecedented in that it ranks the Coninae as a subfamily of a family Conidae that includes other "higher turrid" subfamilies having hollow, hypodermic marginal teeth only and no radular membranes. Their summary argument is this:

Despite the distinctive shell form and high species diversity of the group, we have little anatomical evidence to support the separation of *Conus* at family-level from other higher turrids. We propose only subfamily status for the group. Every anatomical character-state of the conine foregut is shared with species of Clathurellinae and Conorbinae (p. 156).

However, in the section on results of their phylogenetic analysis (fig. 27), the authors state that:

Benthofascis (Conorbinae) and *Conus* (Coninae) (Node 27) share a number of characters. They lack an anterior sphincter to the buccal tube, but have an intermediate sphincter instead. Both have accessory salivary glands and retain an operculum. Additionally both genera show resorption of the inner shell whorls (p. 155).

But the Clathurellinae are noted in Table 3 as having one or two anterior buccal tube sphincters, lacking accessory salivary glands, and either having or lacking an operculum.

In their tabulation of synapomorphies for interior nodes of their cladogram, Taylor et al. (Table 4) indicate two for Node 27, accessory salivary glands present and teeth on the outer shell aperture lip absent. However, the character state matrix (Table 3) also indicates *Genota* to have the latter apomorphy which, if this is correct, should thus be assigned to the preceding Node 26. Like *Benthofascis* and *Conus*, *Genota* also has an intermediate rather than anterior sphincter, but unlike *Benthofascis* and most *Conus* species, it lacks an operculum.

Resorption of inner shell walls, mentioned in the section quoted above but excluded from the Taylor et al. analysis, has long been considered important in classification and the hallmark of the traditional family Conidae (d'Orbigny, 1852; Van Koenen, 1867). It served as a key character to distinguish subfamilies of Conidae in the classic monograph of Cossmann (1896). Inner shell resorption likely represents a suite of interrelated characters apomorphic in Conidae (Kohn, 1990), and its inclusion might strengthen the cladistic analysis.

The development of a formal classification from a phylogenetic hypothesis is always a step that requires subjective judgment. The classification proposed by Taylor et al. departs considerably from the cladogram. It explicitly includes information, mainly radular characters, from taxa

that could not be included in the cladistic analysis, because of the absence of anatomical information. In this classification, the Conoidea comprises the six families Drilliidae, Terebridae, Pseudomelatomidae, Strictispiridae, Turridae, and Conidae. Five of these are monophyletic according to the cladogram, but Turridae is both diphyletic and paraphyletic.

These problems are not readily resolvable, and the classification of the Conoidea remains in a state of flux. As next steps toward more satisfactory solutions we suggest exploring classifications based more closely on the results of Taylor, Kantor, and Sysoev's cladistic analysis than is their proposal, and enhancing their analysis by incorporating additional characters.

Alan J. Kohn
James H. McLean

Literature Cited

- COSSMANN, M. 1896. Essais de paléoconchologie comparée. Cossmann: Paris.
- D'ORBIGNY, A. 1852. Paléontologie française, 1re Sér., 2. d'Orbigny, Paris.
- KOHN, A. J. 1990. Tempo and mode of evolution in Conidae. *Malacologia* 32:55-67.
- MCLEAN, J. H. 1971. A classification of the Family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific. *The Veliger* 14:114-130.
- MORRISON, J. P. E. 1966. On the families of Turridae. *Annual Reports of the American Malacological Union*, 1965:1-2.
- OLSSON, A. A. 1964. Neogene Mollusks from Northwestern Ecuador. Paleontological Research Foundation: Ithaca. 256 pp.
- POWELL, A. W. B. 1966. The molluscan families Speightiidae and Turridae, with general notes on turrid nomenclature and systematics. *Bulletin of the Auckland Institute and Museum* No. 2:1-188.
- SHIMEK, R. L. & A. J. KOHN. 1981. Functional morphology and evolution of the toxoglossan radula. *Malacologia* 20: 423-438.
- VAN KOENEN, A. 1867. Ueber *Conorbis* und *Cryptoconus*, Zwischenformen der Gattungen *Conus* und *Pleurotoma*. *Palaeontographica* 16:159-174.

Reply by Dr. Taylor

We welcome the interest in our paper; the Conoidea are a fascinating group of gastropods and despite the disproportionate attention devoted to the shells of some of the taxa, our knowledge of relationships within the superfamily is very poor. We are very aware of the many inadequacies in our study, principally deriving from the fact that the Conoidea are such a diverse group, so that the species which have been studied anatomically represent only a small subsample of the total diversity. Primarily, we attempted to demonstrate that there are many features of the conoidean foregut which can be utilized in phylo-

genetic analysis. This information was obtained from serial sections of the proboscis and foregut of about 70 species of conoideans, integrated with information from previously published studies. Other organ complexes such as the reproductive system will likely yield further suites of characters but, as yet, remain uninvestigated.

Kohn & McLean advocate using more shell characters and fossil taxa in future analyses. However, we fail to see how the inclusion of fossils would corroborate the phylogeny as they suggest. Our work on turrids and terebrids has shown that shell characters are often a poor guide to internal anatomy. Recent studies of species of the subfamily Crassispirinae have highlighted the fact that animals with rather similar shells e.g., *Ptychobela*, *Funa*, and *Inquisitor* possess very different radulae and foregut anatomies (Kilburn, 1988, 1989; Taylor, in press). Additionally, some species placed in the Mangeliinae on the basis of shell characters turn out to have crassispirine anatomy (Kilburn & Taylor, unpublished). The problem is particularly acute in the Terebridae, where shells can be extremely similar but reveal quite different foregut structures e.g., *Terebra subulata* has a proboscis, hypodermic radula, venom gland, and accessory salivary glands, whereas *Terebra areolata* lacks all these structures. By contrast, a wide range of shell form is found within the Daphnellinae, but species share many common anatomical characters.

The authors highlight the fact that the classification we propose is not a direct transposition from the cladogram. We are of course conscious of the problems of developing a formal classification from the cladogram and very aware that some of the taxa we propose may be paraphyletic. As we were careful to point out (p. 157), the classification we propose represents a conservative compromise, and there are several reasons for this restraint. Primarily, the number of species we analyzed in the cladogram is only a small subset of the total diversity of conoideans, and new combinations of foregut structures are still being discovered (Kantor & Taylor, 1994; Taylor, in press). Moreover, the cladogram was not particularly well resolved or robust, and some nodes are supported by rather few, possibly weak characters. New and continuing work should help resolve some of these problems, although Arnold (1990) has suggested reasons why morphological phylogenies of some groups may never be well resolved.

Perhaps the feature of the classification which has vexed Kohn & McLean the most is the "downgraded" status of Coniinae. The *Conus* species that we have studied have a relatively underderived foregut anatomy (compared to, say, the Mangeliinae and Daphnellinae), which is very similar to that of species in the "borsoniine" group of our Clathurellinae. They have a buccal mass situated at the base of the proboscis, a single accessory salivary gland, acinous salivary glands, and a radular caecum. The venom gland is unchanged in histology anterior to the nerve ring, and the buccal lips are unmodified. The proboscis sphincter lies in an intermediate position within the buccal tube, but